

STEM STRUCTURE OF THE NEW WORLD MENISPERMACEAE

ALBERTA M. W. MENNEGA

SINCE PUBLISHING a taxonomic study on the Menispermaceae (Krukoff & Moldenke, 1938), B. A. Krukoff has remained interested in this family. He has published numerous papers, both alone and as a joint venture with R. Barneby (for a bibliography see Barneby & Krukoff, 1971; see also Krukoff & Barneby, 1970, 1972, 1974, 1978), centering on the tribes Triclisieae and Anomospermeae. The neotropical Tinosporeae were revised by Barneby in 1970; New World species of the tribes Hyperbaeneae and Menispermaceae are currently being studied by others. Rhodes published a revision of *Cissampelos* in 1975.

Various menisperms are important as a source of ingredients for the drug curare. Thinking that still unknown alkaloids might be present in the bark and wood of many species of this family, Krukoff instigated the collection of additional wood samples associated with herbarium vouchers to provide material for both chemical and anatomic studies. The herbarium specimens of most of this material are located at the herbarium of the New York Botanical Garden.

The present study was undertaken at the suggestion of Krukoff, who provided a great number of the wood samples. Because the majority of the samples belong to the Triclisieae and Anomospermeae, the anatomic treatment presented here also centers on these two tribes. Additional information on the Hyperbaeneae, Tinosporeae, and Menispermaceae is based on rather scarce material, as is shown in TABLES 2 and 4 and in the APPENDIX. According to present taxonomy, the New World menisperms comprise five tribes and eighteen genera; this study is based on representatives of thirteen genera.

MATERIAL AND METHODS

All the wood samples used in the present investigation were received dry. Microtome sections were made in the usual way and were stained with safranin. Macerations were effectuated by placing chips in equal parts of glacial acetic acid and hydrogen peroxide at a temperature of 60°C for 24 hours. The macerated material was stained with lactic acid (cotton blue).

Pore diameters were measured tangentially. Due to the great variation in pore size, more attention was given to the widest vessels than to the small or intermediate ones, which are always present. Consequently, the mean width of the widest vessels was calculated rather than the average width of all vessels.

The average of the counts of all vessels in at least ten bundles was calculated instead of the usual average number of vessels per mm². The length of the imperforate elements, of the vessel elements, and of the parenchyma strands was measured in the macerations. For vessel elements and fiber-tracheids the average of 25 counts was taken, for the other elements the average of at least ten counts. The terminology of crystals follows Chattaway (1955, 1956). General terminology follows the International Association of Wood Anatomists' *Multilingual Glossary of Terms used in Wood Anatomy* (1964).

With the exception of *Borismene japurensis* and an unnamed species of *Cissampelos*, the genera and species do not show much variation in microscopic characters. Differences in sizes and numbers of elements may be even greater between species than among genera, as is shown in TABLE 3 by data from all the available material of *Abuta rufescens*. The general uniformity of the microscopic structure makes generic descriptions superfluous and preparation of a dichotomous key impossible. Instead, the presence of characteristic features is listed in synoptic tables, as advocated by Leenhouts (1966). The features included are the shape of the stems (discussed below), the gross aspect of the bark, and the macroscopic characters of the pith (discussed in the next section) (all shown in TABLE 1), and the distribution of crystals and silica grains in the stems (TABLE 2).

STEM MORPHOLOGY

Most menisperms are woody lianas or shrubs with scandent branches; some are slender vines that are woody only at the base. Exceptions include most species of *Hyperbaena* and the Asiatic *Cocculus laurifolius*, which are small trees or shrubs. *Abuta grandifolia* occurs as a shrub, a tree, or a liana.

Irrespective of the plant's habit, a transverse section of its wood usually shows a highly characteristic pattern of abnormal secondary growth consisting of fairly regular consecutive rings or partial rings of vascular bundles separated radially by wide interfascicular rays and tangentially by layers of mixed sclerenchymatous and parenchymatous cells. This special structure was first noticed by Decaisne (1839) in *Cissampelos pareira* and *Cocculus laurifolius*. His findings were later confirmed in representatives of many other menispermaceous genera by numerous botanists, including Radlkofer (1858), Eichler (1864), Blottière (1886), Schenck (1892, 1893), Solereder (1899), Maheu (1902), Diels (1910), Williams (1936), Chalk and Chattaway (1937), Metcalfe and Chalk (1950), Obaton (1960), and van der Walt and associates (1970).

Exceptions to the above-mentioned group of characteristics are known to exist: *Coccinium fenestratum*, a liana from Ceylon (Eichler (1864), Gamble (1881), Solereder (1899), Diels (1910), Zeijlstra (1911)); *Cocculus umbellatus*, from eastern Asia (Zeijlstra, 1911); and *Cissampelos capensis* (Blottière, 1886). Mention should also be made of Decaisne's (1839) statement regarding the structure of a half-inch-wide stem of *Menispermum canadense* in which only one ring of triangular bundles was present. Other exceptions have been mentioned by Dipasupil (1955) for several genera of menisperms

TABLE 1. General characters of the stems.

STEMS

Shape in cross section*

Centric: *Abuta candollei*, p.p., *A. grandifolia*, *A. pahnii*, *A. sandwithiana*, *A. solimoesensis*, p.p., *A. velutina*, p.p.; *Anomospermum bolivianum*, *A. chloranthum*, *A. matogrossense*; *Borismene japurensis*; *Caryomene olivascens*; *Chondrodendron tomentosum*; *Hyperbaena* sp.; *Odontocarya* aff. *wulfschlaegeli*; *Orthomene schomburgkii*; *Sciadotenia eichleriana*, p.p., *S. solimoesana*, p.p.; *Telotoxicum glaziovii*, p.p., *T. krukovi*.

Excentric, not strongly flattened: *Abuta brevifolia*, *A. candollei*, pp., *A. fluminum*, *A. grisebachii*, *A. imene*, *A. obovata*, *A. panurensis*, *A. rufescens*, *A. solimoesensis*, p.p., *A. velutina*, p.p.; *Anomospermum reticulatum*, *A. solimoesanum*; *Caryomene* sp.; *Sciadotenia eichleriana*, p.p., *S. solimoesana*, p.p., *S. toxifera*; *Telotoxicum glaziovii*, p.p., *T. minutiflorum*.

Excentric, strongly flattened, with only 1 or 2 complete rings around pith: *Curarea candicans*, *C. tecunarium*; *Sciadotenia solimoesana*, p.p.; *Chondrodendron microphyllum*, p.p.

Color of wood in transverse section

Yellowish green: *Abuta brevifolia*, *A. obovata*, p.p., *A. pahnii*, *A. panurensis*, *A. sandwithiana*, p.p.

Dull grayish brown: all other species.

BARK

Young twigs velvety, greenish brown: *Abuta rufescens*.

Young twigs neither velvety nor greenish.

Smooth: *Abuta brevifolia*, *A. bullata*, *A. panurensis*; *Anomospermum bolivianum*; *Sciadotenia toxifera*.

Grooved:

Thick, deeply grooved, grooves ca. 4 mm apart: *Anomospermum solimoesanum*.

Thick, superficially and narrowly grooved: *Borismene japurensis*.

Thin, narrowly grooved: all other species.

PITH

Hollow, ca. 5 mm wide: *Caryomene olivascens*, *Caryomene* sp.

Solid, 5 mm or more wide: *Abuta grandifolia*, p.p., *A. rufescens*; *Anomospermum bolivianum*; *Borismene japurensis*; *Elephantomene eburnea*; *Telotoxicum krukovi*.

Solid, usually 1.5–3 mm wide: all other species.

*Not all specimens cited in the Appendix could be assigned to a category, either because the pieces of large stems did not allow visualization of the section of a complete trunk or because only sections were present.

from the Philippines, and by Obaton (1960) for a liana from the Ivory coast.

It has generally been assumed (Record & Hess, 1943) that among New World representatives of the family no exceptions from the "normal" pattern occur. In the present investigation, however, three stems—one of a species of *Cissampelos* (as yet unnamed) and the other two of *Borismene japurensis*—also showed a different type of secondary growth.

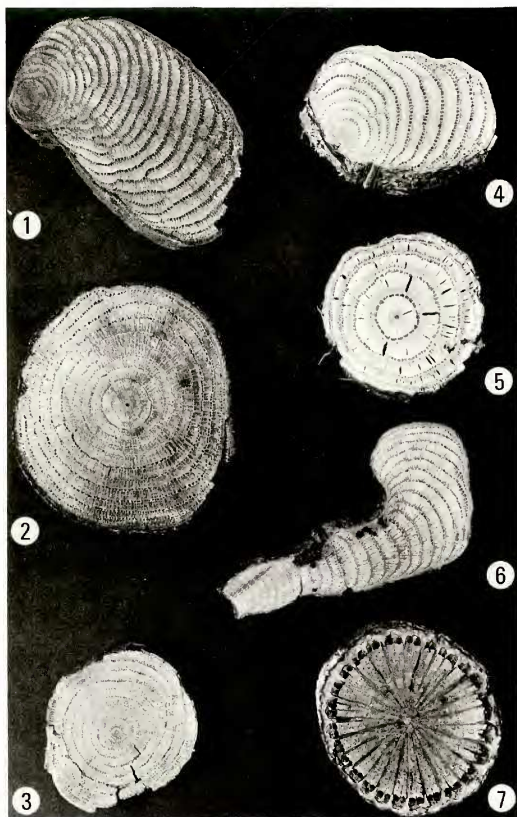
The typical pattern referred to above is illustrated by transverse sections

TABLE 2. Occurrence of silica and crystals.

TRIBE	TAXON	PRESENCE OF SILICA GRAINS	ABSENCE OF CRYSTALS	CRYSTAL TYPES			
				Large, rhomboid; solitary or twin	Small, rhomboid; one per cell	Rhomboid; large and small in same cell	Small, acicular
TRICLISIAE	<i>Curarea candicans</i>			+ 1	+++ 1,2		
	<i>Curarea tecunarium</i>		p.p.		+ 1,2 p.p.		
	<i>Curarea toxicifera</i>			++ 1,2	+++ 1,2	+ 1	
	<i>Chondrodendron microphyllum</i>				+++ 1,2	+++ 1,2	
	<i>Chondrodendron tomentosum</i>			+ 1,2	++ 1,2	+++ 1,2	
	<i>Sciadotenia eichleriana</i>			++ 1,2		+++ 1,2	
	<i>Sciadotenia paraensis</i>			++ 1,2			
	<i>Sciadotenia solimoesana</i>			+ 1,2			
	<i>Sciadotenia sprucei</i>			+ 2			
	<i>Sciadotenia toxifera</i>			++ 1,2	+2	+1	
HYPER- BAENAE	<i>Hyperbaena domingense</i>			+2	+++ 2	+ 2	
	<i>Hyperbaena</i> sp.			++ 1,2	+++ 2	++ 2	+++ 2
	<i>Telitoxicum glaziovii</i>			++ 1		+ 2	
	<i>Telitoxicum krukovi</i>		—				
	<i>Telitoxicum minutiflorum</i>		p.p.	+ 1			
	<i>Abuta brevifolia</i>			+ 1	+ 1		
	<i>Abuta candollei</i>			+ 1			
	<i>Abuta colombiana</i>			+ 1			
	<i>Abuta fluminum</i>			++ 1	++ 2		
	<i>Abuta grandifolia</i>		p.p.	+ 1			
	<i>Abuta grisebachii</i>						
	<i>Abuta imene</i>			++ 1,2			

ANOMOSPERMEAE	<i>Abuta obovata</i>		+ 1			
	<i>Abuta pahnii</i>		+++ 1,2			
	<i>Abuta panurensis</i>		+ 1			
	<i>Abuta rufescens</i>	p.p.	+ 1,2	+ 2		
	<i>Abuta sandwithiana</i>		+ 1	++ 2		
	<i>Abuta solimoesensis</i>	—				
	<i>Abuta velutina</i>	—				
	<i>Caryomene olivascens</i>		+ 1			
	<i>Caryomene</i> sp.				+ 1	
	<i>Anomospermum bolivianum</i>	++ 2	—			
	<i>Anomospermum chloranthum</i>		++ 1			
	<i>Anomospermum chloranthum</i> subsp. <i>occidentale</i>		++ 1			
	<i>Anomospermum matogrossense</i>		++ 1,2		+ 1	
	<i>Anomospermum reticulatum</i>		+++ 1,2			
	<i>Anomospermum reticulatum</i> subsp. <i>dielsianum</i>		+ 1			
	<i>Anomospermum solimoesanum</i>	++ 2,3	—			
	<i>Orthomene prancei</i>		+ 1			
	<i>Orthomene schomburgkii</i>		++ 1,2			
	<i>Elephantomene eburnea</i>		+ 1		+ 2	
TINO- SPOREAE	<i>Odontocarya</i> aff. <i>wulfschlaegelii</i>		++ 4	+ 4	++ 4	++ 4
	<i>Borismene japurensis</i>		+++ 4			++ 4
MENI- SPERMEAE	<i>Cissampelos fasciculata</i>		+ 1	++++ 2	++ 1	
	<i>Cissampelos pareira</i>		+++ 1	++++ 2	++ 1	
	<i>Cissampelos</i> sp.				+	+++ 4

Explanation of symbols: (—) crystals absent, (p.p.) crystals only present in part of the specimens, (+, ++, +++, +++) the relative amount of crystals. Tissues in which the crystals occur: (1) parenchyma cells or sclerotic tissue of the "connective bands," (2) interfascicular rays, (3) vascular parenchyma bands, (4) wide medullary rays, particularly where they border on the fiber tissue.



FIGURES 1-7. Transverse sections of menisperm stems, $\times 1$: 1, *Abuta imene*, stem excentric; 2, *Telitoxicum glaziovii*, stem centric; 3, *Orthomene schomburgkii*, stem centric; 4, *Sciadotenia toxifera*, stem excentric; 5, *Chondrodendron tomentosum*, stem centric; 6, *Curarea tecunarium*, stem strongly excentric and comma shaped in cross section; 7, *Borismene japurensis*, showing wedge-shaped vascular bundles (instead of characteristic successive layers of bundles).

of stems of various genera (FIGURES 1–6, 20, 21). With the exception of *Borismene* (FIGURE 7), all show the concentric rings or partial rings of vascular bundles separated radially by rather wide interfascicular rays that are not continuous from one ring to the next. Tangential bands of connective tissue composed of parenchymatous and sclerotic cells separate one ring of bundles from the next.

Although spacing and width of the bundles are fairly regular in cross section, this is not the case for the outline of the stem sections. Stems can be strongly excentric, winged on one side, or even much flattened, as can be seen in FIGURES 1, 4, and 6. Maheu (1902) mentioned excentric growth of the stems for *Abuta rufescens*, *A. selleana*, *Anomospermum grandifolium*, *A. schomburgkii*, and *Chondrodendron tomentosum*. Schenck (1893) published a drawing of a double-winged stem of *Abuta rufescens* and stressed the fact that the form of a sectioned stem is not constant over its entire length. Some lianas that grow very thick and long (e.g., *A. rufescens*) may show different shapes in different places. Dimensions of the transverse sections, shown in the list of material studied (APPENDIX), give an idea of the sizes and shapes of the stems; where two dimensions are given, the form is elliptic.

WOODS WITH TYPICAL STRUCTURE

PITH. The pith is usually relatively small (1–3 mm in diameter), but in some cases it is up to 7 mm wide (see TABLE 1); sometimes the central part is hollow. An inner and an outer pith can usually be recognized. The inner part consists of a central core of large, more or less isodiametric, thin- or thick-walled parenchyma cells with large intercellular cavities (FIGURES 12–15). In dried material the cells are empty or are filled with starch; occasionally they contain crystals. Solitary or clustered stone cells may be found scattered among the parenchymatous cells. Secretory sacs, which Solereder (1899, 1908) noted for several, mostly Old World genera and which Santos (1928, 1931) mentioned for *Tinospora* sp., *Archangelisia flava*, and *Anamirta cocculus* (all collected in the Philippines), were seen only in material of *Abuta rufescens* and *Cissampelos* sp.

The inner pith gradually changes into the outer pith, where the parenchyma cells become smaller in diameter and more elongate in form; often septa are formed. Fiber "caps," originating in the pith opposite the protoxylem of the bundles and resembling the fiber "caps" on the outside of the phloem of the bundles, are characteristic of this zone. These fibers may be restricted to a small number, forming an unobtrusive group embedded among the parenchyma cells (FIGURE 14), or they may form crescent- or dome-shaped masses, as illustrated in FIGURES 13 and 15.

In *Borismene japurensis* and an unidentified specimen of *Cissampelos*, both characterized by a mode of growth different from the other menisperms, the parenchyma cell walls of the pith are not lignified and the cells contain numerous small, spindle-shaped, acicular crystals. The pith of *Borismene* is different in other aspects as well, as is discussed below.

VASCULAR BUNDLES. The number of vascular bundles around the pith varies considerably, usually fluctuating between 25 and 40, although 88 bundles

TABLE 3. Stem features in specimens of *Curarea tecunarium* (tribe Triclisieae) and *Abuta rufescens* (tribe Anomospermeae).

SPECIMEN NUMBER	DIMENSIONS (in cm) OF CROSS SECTION WOOD SAMPLE	LENGTH AND WIDTH (in mm) OF BUNDLES	NUMBER OF VESSELS PER BUNDLE (mean and range)	TANGENTIAL DIAMETER (in μm) OF WIDEST VESSELS	NUMBER OF BUNDLES AROUND PITH
<i>Curarea tecunarium</i>					
Uw 18054	1×3.5	2.6×0.4	18 (12 to 25)	170-240	
Uw 18678	1×3.5	1.7×0.4	15 (8 to 19)	200	
Uw 18679	a	$2.3 \times 0.3-0.4$	17 (10 to 31)	190-250	
Uw 18680	a	$2-2.8 \times 0.4-0.5$	16 (8 to 28)	200-230	
Uw 18681	a	3.5×0.3	22 (15 to 28)	170-240	
Uw 18682	1.5×2.5	$2.3-2.8 \times 0.35-0.45$	18 (8 to 30)	200-240	
Uw 18683	2×6	$3-4 \times 0.3-0.48$	29 (22 to 38)	160-190	
Uw 18684	2×6	$1.8 \times 0.35-0.55$	15.5 (10 to 25)	180-230	
Uw 18685	2×7	$2.8-3.5 \times 0.5-0.75$	30 (25 to 33)	200-220	
Uw 18686	1.5×7	$2.2-3 \times 0.4-0.5$	15 (7 to 22)	200-220	
Uw 18687	2×10	$2-2.5 \times 0.3-0.4$	14.3 (9 to 21)	230-280	
Uw 18688	a	$2.5 \times 0.35-0.5$	17 (14 to 21)	200-250	
Uw 18689	a	$2.7 \times 0.2-0.5$	12 (8 to 20)	230-300(-350)	
Uw 18690	a	$2.4-3 \times 0.25-0.4$	19 (10 to 26)	200-240	

	Uw 18692	0.5 × 6	1.5-1.7 × 0.3-0.4	11 (5 to 15)	180-200	
	Uw 18693	a	2 × 0.4-0.6	15 (10 to 27)	160-220	
	Uw 18747*	3 × 6	3 × 0.35-0.45	5 (2 to 9)	300-350	
Abuta rufescens	Uw 12356	1.4 × 1.4	2.5 × 0.24-0.3	6 (2 to 10)	80-120	50
	Uw 18058	2 × 4.5	2.3-2.5 × 0.4-0.5	10 (7 to 13)	300-360	80
	Uw 18071	1.5 × 4.5	2.2-2.5 × 0.45	9 (3 to 18)	300-360	62
	Uw 18079	2 × 5-6	2.5 × 0.5-0.6	6 (1 to 9)	300-360	31
	Uw 18519	1 × 1	1.1 × 0.4	4 (1 to 8)	120-140	60
	Uw 18623	1.3 × 6	2.2 × 0.45	9 (6 to 11)	260-330	>45
	Uw 18660	b	2.5-3.2 × 0.4-0.6	11 (5 to 15)	260-325	a
	Uw 18661	4 × 10	2.2-2.8 × 0.45	9 (5 to 13)	300-350	a
	Uw 18662	1 × 2	2-2.3 × 0.35-0.5	10 (3 to 17)	250-300	46
	Uw 18663	a	2-2.25 × 0.3-0.45	10 (4 to 15)	230-300	a
	Uw 18665	3 × 6	1.7-2 × 0.4	5.5 (3 to 9)	250-300	a
	Uw 18730	3.5 × 4.5	1.4-1.9 × 0.3-0.4	5 (2 to 9)	250-320	45
	Uw 18926	1.5 × 4.5	2 × 0.35-0.5	7 (4 to 10)	250-360	55
	Uw 21098	3.5 × 4	1.8-2.6 × 0.3-0.4	8 (2 to 14)	270-350	73

Explanation of symbols: (a) pith absent or only sections available, (b) strip of a stem over 7 cm wide.

*Probably not this species but an *Abuta*, as implied by the figures and also by the cross-sectional outline of the stem and the texture of the bark.

were recorded in *Elephantomene eburnea* and 44 in *Chondrodendron microphyllum*. An illustration of the considerable variation of this character within one species is given in TABLE 3 for *Abuta rufescens*, for which the numbers range between 31 and 80.

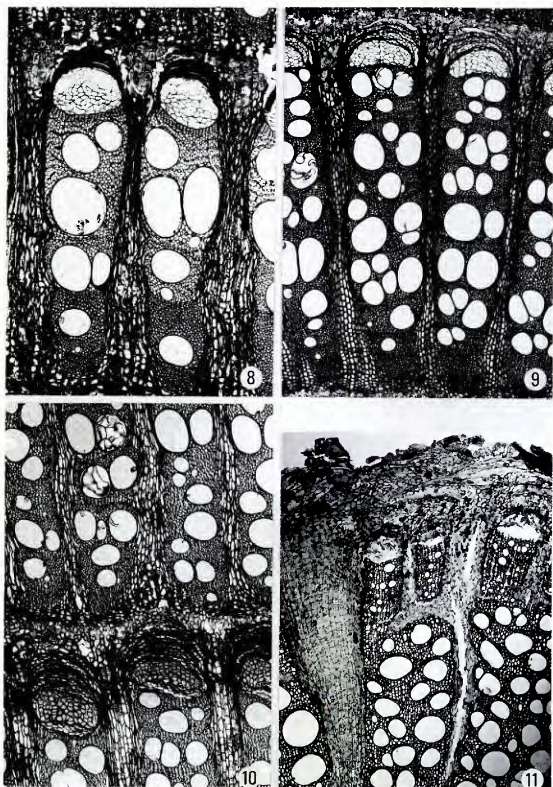
The medullary (primary) and secondary interfascicular rays separating the bundles of each ring are often very wide and very high, with considerable variation within each sample (e.g., in *Anomospermum reticulatum* (Uw 18614)). The wider rays are 25 cells (525 μ m) wide and over 2 cm high; the narrower ones are only 11 cells (200 μ m) wide. The cells are mainly procumbent and are of irregular dimensions as seen in radial and tangential sections. They are often filled with starch and may also contain crystals of different forms, or silica grains as is the case in two species of *Anomospermum* (see below). The rays are not continuous from ring to ring (FIGURES 16, 17, 20, 21).

As seen in transverse section, the vascular bundles are wedge shaped to nearly rectangular. Radially they measure from 1.5 to 5.5 mm; their widest tangential dimensions range from 0.3 to 0.8 mm. Usually some variation occurs within a stem, particularly in one that is excentric or otherwise irregular (FIGURES 1, 4).

In the first-formed ring of vascular bundles, the oldest, obliterated cell layers of the phloem are surrounded by one layer of thin-walled parenchymatous cells. Outside of these cells, there is a thick, crescent-shaped "cap" of thick-walled sclerenchymatous fibers. Beyond the "caps" a continuous cortical band of parenchyma stretches over both the "caps" and the medullary rays. In this zone the cambium is generated; this gives rise to the next ring of bundles. The difference between the first and the second and subsequent rings is that in the first ring the fiber "caps" are restricted to the connective tissue. The consecutive rings of bundles are separated from each other by a connective tissue consisting of a layer of parenchyma, a two- to four-cell-wide layer of stone cells, and an outer layer two to six cells wide of parenchyma. The layer of stone cells widens over the interfascicular rays and penetrates, wedgelike, into these rays usually as far as the vascular cambium (see FIGURES 8–10, 16).

The woody part of the bundles is composed of vessels, fiber-tracheids, and axial parenchyma; rays are extremely scarce. The radial dimensions of the woody part are highly variable, although they generally tend to be shorter in the *Anomospermeae* (1–2.5 mm) than in the *Trielisiaceae* (2.5–5 mm) (see FIGURES 20, 21; TABLE 3). In the phloem portion of the bundles, tangential bands of sieve tubes and companion cells occur alternately with bands of parenchyma cells; fibers are always absent. The oldest peripheral layers are shaped and composed of strongly flattened sieve tubes and intact paren-

FIGURES 8–11. Transverse sections, $\times 28$: 8, *Abuta rufescens* (Uw 18661), showing two vascular bundles with few large, solitary vessels and few small ones, active phloem parts "capped" by several obliterated cell layers, connective tissue on abaxial side consisting mainly of stone cells penetrating into interfascicular rays up to cambial



zone; 9, *Curarea tecunarium* (Uw 18682), with vessels more numerous and smaller; 10, *Sciadotenia eichleriana* (Uw 18658), showing same type of bundles as *Curarea*, fingerlike thin tyloses present in some vessels; 11, *Cissampelos* sp. (Uw 18072), showing different type of growth, without successive layers (wide, wedge-shaped interfascicular rays continuous from pith to bark; woody part has split during growth of stem).

chyma, resulting in a banded appearance of the phloem "cap" (see FIGURES 9 and 10). Sizes of the phloem portion vary from 500 to 700 μm tangentially and from 300 to 500 μm radially.

VESSELS. Although the vessels are mainly solitary, they sometimes occur in radial multiples of two, or in tangential groups of two or three with or without direct contact; the tangential arrangement is frequently continuous from one bundle to the next (FIGURE 21). In each bundle wide and narrow vessels are intermingled. Vessels are often absent in the adaxial part of a bundle, or sometimes only one or two extremely narrow ones are to be found; this feature occurs more frequently in the Anomospermeae than in the Triclisieae. The narrowest vessels are about 40 μm wide, the widest 350–400(–500) μm . The number of vessels per bundle is rather variable within a sample, but an average can be established with some confidence from a survey of a great number of bundles seen in cross section. These averages range from 14 to 34 per bundle for genera of the Triclisieae, and from 4 to 19 for the Anomospermeae (see TABLE 4, FIGURES 20, 21). A possible relation between taxonomy and the number and width of the vessels is discussed below.

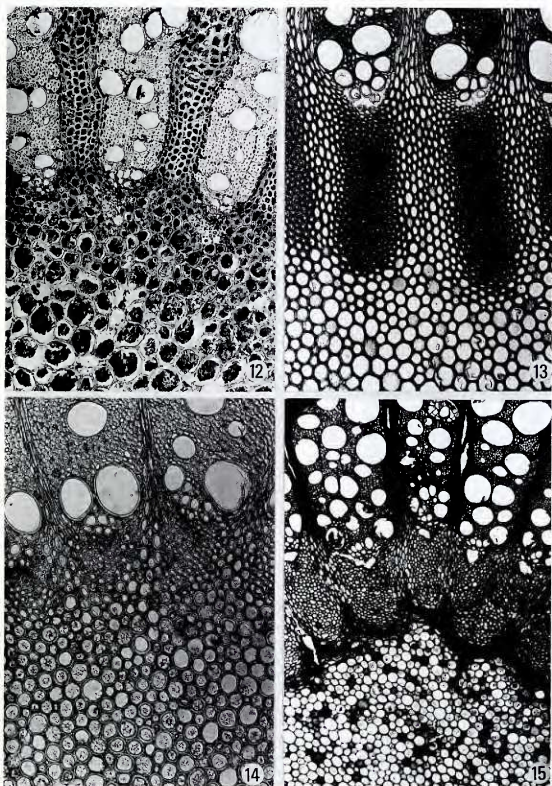
The perforations of the vessel elements are exclusively simple, with the perforation plates nearly horizontal. Intervascular pitting is irregular, with the pits from 6 to 11 μm wide and the apertures enclosed or confluent; near the end of a vessel member there are always clusters of very large, elongated

TABLE 4. Vessel characters.

TRIBE	GENUS	AVERAGE NUMBER OF VESSELS PER BUNDLE (range)	TANGENTIAL DIAMETER OF WIDEST VESSELS (in μm)
Triclisieae	<i>Chondrodendron</i> (2)*	14 to 34	300
	<i>Curarea</i> (3)	15 to 29	250
	<i>Sciadotenia</i> (5)	20 to 28	240
Hyperbaeneae	<i>Hyperbaena</i> (4)	8 to 24	210
Anomospermeae	<i>Telotoxicum</i> (3)	3.5 to 13 (to 40)	300–400
	<i>Abuta</i> (15)	4 to 19	350
	<i>Caryomene</i> (2)	16 to 19	350–400
	<i>Anomospermum</i> (5)	5 to 8	350–400
	<i>Orthomene</i> (1)	6 to 10	350
	<i>Elephantomene</i> (1)	4 to 9	500
Tinosporeae	<i>Odontocarya</i> (1)	14	400
	<i>Borismene</i> (1) [†]		400
Menispermeae	<i>Cissampelos</i> (2)	25 to 31	230
	<i>Cissampelos</i> sp. [†]		220

*The number of species investigated is cited in parentheses.

[†]Due to different stem structure in *Borismene* and one (unidentified) specimen of *Cissampelos*, data for number of vessels per bundle are not applicable.



FIGURES 12-15. Details of pith region: 12, *Abuta sandwithiana* (Uw 18739), $\times 70$; 13, *Elephantomene eburnea* (Uw 21079), $\times 70$, adaxial bundle "caps" of thick-walled fibers strongly developed; 14, *Sciadotenia sprucei* (Uw 18745), $\times 70$, pith cells relatively thick walled, adaxial "caps" unobtrusive; 15, *Chrondrodendron tomentosum* (Uw 18694), $\times 28$, pith cells thin walled, adaxial bundle "caps" well developed.

pits with narrow borders (FIGURE 19). Vessel members average 230–500 μm long (including the short tails, if present). Tyloses occur frequently and are generally thin walled and fingerlike (FIGURES 9, 10, 16).

VASCULAR TRACHEIDS. Vascular tracheids of the same length as the vessel members are occasionally present, but in macerations they are often difficult to distinguish from the shortest fibers.

FIBER-TRACHEIDS. The fiber-tracheids are nonseptate, with numerous small, bordered pits on radial and tangential walls. Their mean tangential diameter is 16–24 μm . The walls are mostly 4–5 μm thick. The length varies considerably in each species, ranging from 400 to 1900 μm and averaging between 700 and 1300 μm .

PARENCHYMA. The axial xylem parenchyma of all species (with the exception of the aberrant *Borismene japurensis* and the unnamed species of *Cissampelos*) consists of numerous one-cell-wide, wavy, tangential bands. Sometimes vasicentric strands are also present, but they seldom form a complete ring. Strands are usually composed of two cells, but four-celled strands also occur; their mean length is 350 μm (range, 270–460 μm).

RAYs. Rays are very rare in the bundles, occurring only in the widest abaxial portions of the largest ones (e.g., *Curarea toxifera*); they are uniseriate and consist of upright cells.

WOODS WITH A DIFFERENT STRUCTURE

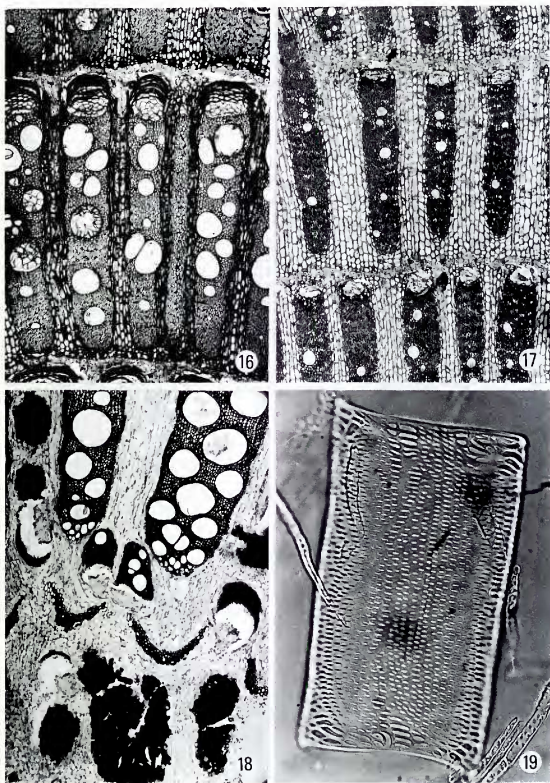
***Borismene japurensis* (Martius) Barneby**

FIGURES 7, 18.

MATERIAL: *J. Schunke* V. 5388 (Uw 20524), Peru. Stem diameter 3.8 cm, centric; bark grayish brown, 3 mm thick, the rhytidome with superficial, narrow grooves. *Plowman & Schunke* 7547 (Uw 25678), Peru. Liana 8 m tall; trunk terete, 2 cm in diameter; bark similar to that in preceding sample.

Pith narrow, 3 mm wide, consisting of large, unlignified parenchymatous cells; dispersed among these cells are large, isolated or clustered stone cells. A number of small, irregularly distributed medullary bundles, 500 by ca. 200 μm , occur at the periphery of the pith in one sample (Uw 20524). These bundles are inversely oriented but are otherwise normally developed (FIGURE 18). The pith is surrounded by 27 main bundles in Uw 20524 and 20 in Uw 25678; at the circumference of the stem there are about twice that number of phloem "caps" due to dilation that results in a splitting of the main bundles near the pith. At this level in Uw 20524, the wood of all bundles is penetrated by transverse intrusions of parenchyma from the medullary rays. Beyond this irregular region, which contains only a few narrow vessels, a new wide ray is formed that divides the original bundle in two or sometimes three equal parts, whereupon normal growth is resumed. Although the intrusion of a few parenchyma cells may repeat itself at intervals, in the material at hand dilation was apparently not yet sufficient to induce renewed splitting of the bundles.

The elements of the wood are similar to those described in the preceding



FIGURES 16-19. 16, 17, transverse sections of *Abuta grandifolia*, $\times 28$: 16, Uw 18688, liana; 17, Uw 3361, small tree. 18, *Borismene japurensis* (Uw 20524), pith with inverted bundles and first ring of bundles, $\times 28$. 19, *Orthomene schomburgkii* (Uw 18075), maceration showing vessel member with large, elongated pits near perforation, $\times 180$.

paragraph. Vessels are up to 400 μm wide; thin- or thick-walled tyloses occur; pits are of irregular sizes, 8–16 μm wide, often with very large apertures. The fiber-tracheids are 24–30 μm wide, and the lumen is large. The medullary rays are from 10 to 40 cells wide (250–1200 μm), and the cells contain a large number of small and large crystals, mainly small, acicular ones in the interior ray cells, and rhombic ones in the cells adjacent to the bundles. Within the bundles uniseriate rays are occasionally present. One-cell-wide bands of axial parenchyma are scarce, short, and scattered.

The phloem of the bundles is capped by an arc of sclerenchyma; where the bundles are split, paired or tripled phloem is capped by a single arc.

***Cissampelos* sp.**

MATERIAL: *Barquero 1970/201* (Uw 18072), Costa Rica. Stem diameter 1 cm, centric; bark very thin, smooth.

The narrow pith is 800 μm wide and consists of large parenchymatous cells with thin, unlignified walls. The cells become gradually smaller near the outer part. The groups of fiberlike cells opposite the primary xylem are small. The pith is surrounded by 13 vascular bundles 3.6 mm by 800–1100 μm , some of which are radially divided by an ingrowth of parenchymatous cells. The bundles are separated by broad, wedge-shaped, nonlignified medullary rays up to 1400 μm wide. The vessels are often more or less tangentially arranged in rows of 4 to 6 and have a maximum width of 200–220 μm ; tyloses are absent. Axial xylem parenchyma is scarce and in tangential patches or irregular, very short, tangential bands.

This species differs from material of *Cissampelos pareira* L. (Uw 5437) and another (unidentified) specimen (*Gill 20a*) in the absence of successive rings of bundles, in the splitting of some of the bundles, and in the unlignified cells of the pith and medullary rays. The numerous large and small rhomboid crystals found in the interfascicular rays and the connective tissue of these two specimens are also absent in the specimen described above.

OCURRENCE OF CRYSTALS AND SILICA

Crystals of various forms are of general occurrence in menisperms; silica inclusions, on the contrary, are very rare and in the present material are restricted to two species of *Anomospermum*: *A. bolivianum* and *A. solimoesanum*. In these two species the silica grains are mainly in the cells of the parenchyma bands of the vascular bundles and, to a lesser degree, in the cells of the interfascicular rays; in the other genera and in other species of *Anomospermum*, crystals never occur in the cells of the bundle parenchyma but are found in those of the connective tissue and the interfascicular rays.

The variation in the form of the crystals was described by Solereder (1899, 1908), who reported their presence in the tissues of the leaves. Krafft (1907), in his thesis on the anatomy of the leaves of the Menispermaceae, stressed the importance of the occurrence of various types of crystals, such as spiculae and the small and large rhomboid calcium oxalate crystals. In addition, he mentioned the probability that the presence of sclerotic elements and the for-

mation of crystals are related since the two often occur close together. Such a relation was also found in the wood specimens examined in this study. Crystals are most frequently found in the parenchymatous cells bordering the sclereids of the conjunctive tissue.

In a single species can be found large, single rhomboid crystals of calcium oxalate completely filling the cells, twin crystals or one large and several small ones in the same cell, or one or two rodlike or acicular crystals (terminology follows Chattaway, 1955, 1956). Alternatively, there may be such a profusion of small crystals that they might be called crystal sand.

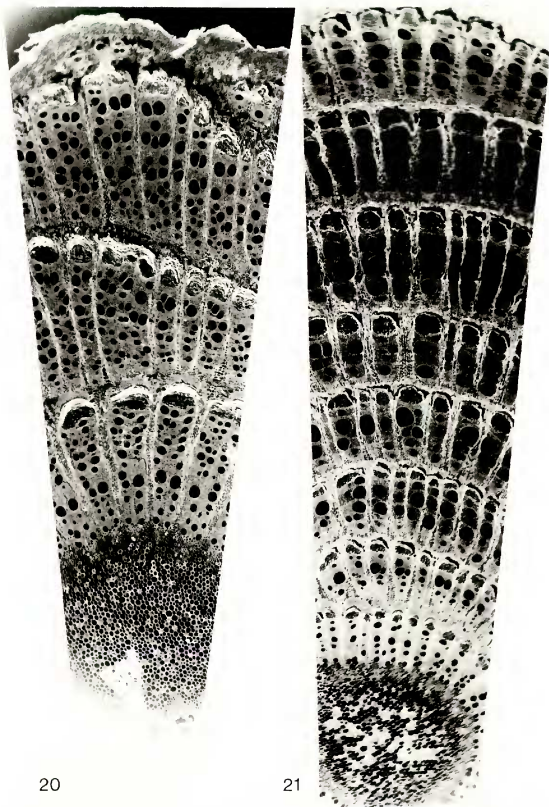
As is seen in TABLE 2, the presence and quantity of a special type of crystal is characteristic of some genera or species; for example the abundance of nearly all types of crystals in *Chondrodendron*, as well as in two species of *Curarea*, *Sciadotenia eichleriana*, *Cissampelos fasciculata* and *C. pareira*, *Hyperbaena*, and *Odontocarya* aff. *wulfschlaegelii*. Small, acicular, spindle-shaped crystals are particularly characteristic of *Borismene* and *Cissampelos* sp.

DISCUSSION

In the Menispermaceae it is not possible to separate the genera on the basis of their wood anatomy. One can, however, suggest tribal characteristics that make it possible to assign material to either the Anomospermeae or the Triclisieae, and perhaps to the Hyperbaeneae. *Borismene*, however, stands by itself.

When this study was initiated with limited material of the tribes Triclisieae and Anomospermeae, it appeared that *Chondrodendron*, *Curarea*, and *Sciadotenia* formed one group and *Abuta*, *Anomospermum*, *Caryomene*, *Orthomene*, and *Teletoxicum* another, as shown in FIGURES 20 and 21. In the Triclisieae the vascular bundles, as seen in cross sections of the stems, are mostly relatively long, narrow, and wedge shaped adaxially, containing numerous vessels of various widths (maximum width usually 250–300 μ m). Besides the three New World genera represented by many samples, a specimen of *Tiliacora funigera*, also belonging to tribe Triclisieae, has the same type of bundles. The Anomospermeae, on the other hand, are characterized by bundles with less radial extension and more rectangular form; the number of vessels is smaller, and some have a larger (300–400 μ m) diameter. The initial impression of two structural types was somewhat altered when more material became available, because individual samples of some species represented by a large number of specimens did not fit the overall picture of the tribes.

The discrepancies among samples are partly due to the different habits of the individual plants, such as shrub or tree versus liana (see below). They may also arise from sampling different portions of a plant—for example, a thick, full-grown stem of a liana or a younger, less-developed flowering branch—particulars that are generally not mentioned on the accompanying labels. In other cases (e.g., with *Chondrodendron microphyllum* (Uw 18061) and *Curarea tecunarium* (Uw 18747) of the Triclisieae, and *Teletoxicum*



FIGURES 20, 21. Transverse sections, $\times 16$: 20, *Sciadotenia paraensis* (Uw 18068), showing pattern characteristic of tribe Triclisieae; 21, *Abuta grisebachii* (Uw 18666), showing pattern characteristic of tribe Anomospermeae.

minutiflorum (Uw 18673) and *Anomospermum bolivianum* (Uw 18672, of the Anomospermeae) no obvious reason could be found for the diverging patterns. Confusion of herbarium and wood samples cannot always entirely be excluded. It is sometimes particularly difficult when collecting material of lianas to sort out the tangled masses of stems dangling from the trees from the flowering or fruiting branches that may be growing farther away. In Gill's material of *Curarea tecunarium* (Uw 18747 = Gill 35), such an error has most likely taken place: not only are the number and the width of the vessels different from those of the other samples (see TABLE 3), but the form of the stem—comma shaped as seen in cross section—is more suggestive of *Abuta* (*Curarea* has very flat, strap-shaped stems). In the other specimens cited above, confusion during collection is not as likely because the data are intermediate between the two groups.

In spite of the exceptions, if one considers the large number of samples seen in both tribes, the impression seems justified that a general anatomic trend exists in each of the two tribes. This trend can be used with some confidence as a means to assign a specimen to one tribe or the other.

A circumscription of these two tribes is not flawless, and the delimitation of the Hyperbaeneae in a similar way is even more uncertain. From the scarce material available, supplemented by data forwarded by the late Dr. L. Chalk for samples of *Hyperbaena domingensis* (a liana) and *H. winzerlingii* (a tree), *Hyperbaena* might be considered to be an intermediate genus. The average number of vessels per bundle is from 15 to 25, and the average size for the widest vessels 150(–200) μm , but often less. The largest vessel size, together with the same average number of vessels per bundle, can also be found in specimens belonging to genera of the Triclisieae, to which members of tribe Hyperbaeneae show the closest affinities.

Structural affinities to the Triclisieae are also shown by species of *Cissampelos*, a genus of the tribe Menispermeae. Of the three stems investigated, two resemble the Triclisieae in number of vessels (average, 25 to 31 per bundle) but differ in having a slightly lower value for the greatest width (ca. 200 μm). A third specimen, *Barquero* 1970/201, does not conform to the others because only one ring of bundles is formed. Although the diameter of the sample is only 1 cm, in other samples this size a second ring is usually present. Furthermore, the splitting of some of the bundles by radial parenchyma intrusion is indicative of another type of secondary growth. Solereder (1899, citing Hérail) and Schenck (1893) also doubted the constancy of the menisperm type of abnormal secondary growth in some species of *Cissampelos*.

The usual menisperm pattern is also absent in tribe Tinosporeae, which is represented in the New World by four genera. Of these, wood samples were available only for one species of *Odontocarya*, and for *Borismene*, a monotypic genus. Unfortunately, the specimen of *Odontocarya wulfschlaegeli* was very small and was in poor condition due to fungal attack. This species was illustrated and briefly described by Eichler (1864) under the name *Somphoxylon Wulfschlaegeli*. The stem that he saw was of the same diameter as the present sample. In both stems only one ring of bundles has been formed.

The interfascicular rays are very wide—wider than usual in stems of this size. The bundles are nearly triangular, thus resulting in a cross-sectional pattern differing from the one usually present in menisperms. Material of larger-sized stems (if these plants grow any larger—which is questionable since other species described by Barneby (1972) are also stated to have stems ca. 1 cm in diameter) will be necessary for elucidating the problem should the wood structure not follow the usual trend. On the other hand, in *Borismene* (FIGURE 7), the other representative of this tribe, there is clearly another form of secondary growth—one without supernumerary cambia. Radial splitting of the bundles by parenchymatous plates, described above in one sample of *Cissampelos* (Uw 18072) and in *Borismene* (Uw 20524, 25678), was noted by Obaton (1960) for *Rhigiocarya racemifera*, an African liana of the tribe Tinosporeae.

A mode of growth even more similar to that occurring in *Borismene* is shown by the Philippine *Stephania japonica* of the tribe Menispermaceae, recorded by Dipasupil (1955) as having tangential intrusions of parenchyma from the medullary rays. Decaisne (1839) described and illustrated the wood of a half-inch-wide stem of *Menispermum canadense* as having secondary growth normal although with very wide medullary rays.

In the tribe Anamirteae, not represented in the New World, *Anamirta* shows the familiar menisperm structure, although *Coscinium fenestratum* has a normal uninterrupted woody cylinder dissected radially by very wide medullary rays. Apparently in the Anamirteae, the Tinosporeae (including the Fibraureae according to Barneby (1972)), and the Menispermaceae, some species or perhaps genera do not follow the general structural trend, while in the Triclisieae (with the possible exception of *Pycnarrhena manillensis*, studied by Dipasupil (1955)), the Anomospermeae, and the Hyperbaeneae the wood always shows the concentric layers of bundles in cross section.

RELATION BETWEEN HABIT AND ANATOMY

In families that include numerous climbing species among their members, plants of a single species may grow either as a tree or as a liana. In the Menispermaceae this is the case with *Abuta grandifolia*, a species very well represented among our material (see APPENDIX). To correlate variation in anatomic characters with habit, data were compiled for vessel width, length of vessel elements, length of fiber-tracheids, and ratio of these lengths for specimens for which the growth habit was known. The results are shown in TABLE 5.

One of the obvious dissimilarities between the arborescent and the vining specimens of *Abuta grandifolia* is the difference in vessel width, shown in FIGURES 16 and 17: narrower vessels occur in the trees than in the lianas. The length of the vessel elements is about the same in both groups. The fiber-tracheids, on the contrary, show a distinct difference in average length, being longer in the arborescent specimens. Apparently length of the imperforate elements is habit related, while that of the vessel members is not. The ratio of fiber-tracheid length to vessel member length also differs with habit, ranging from 3.7 to 5 for the trees and from 2 to 3.1 for the lianas. In the

TABLE 5. Comparison of *Abuta grandifolia* growing as a shrub or tree and as a liana.

SPECIMEN NUMBER	HABIT	RANGE OF WIDEST VESSELS (in μm)	MEAN LENGTH AND RANGE (in μm)		RATIO OF FIBER- TRACHEID LENGTH TO VESSEL LENGTH
			VESSELS	FIBER-TRACHEIDS	
Uw 1612	Shrub	40-70	350 (170-550)	1400 (1150-1625)	4.0
Uw 3361	Treelet	30-90	350 (150-480)	1660 (1250-1840)	4.8
Uw 3341	Shrub	40-70	320 (180-440)	1296 (1000-1700)	4.0
Uw 18750	Tree	30-120	283 (140-430)	1405 (1050-1950)	5.0
Uw 18753	Tree	110-140	375 (225-540)	1790 (1375-2150)	4.8
Uw 18754	Tree	60-120	294 (150-440)	1560 (900-2250)	5.3
Uw 18755	Tree	40-100	314 (250-500)	1600 (1075-1980)	5.1
Uw 18757	Shrub	30-100	366 (300-485)	1570 (1250-1900)	4.3
Uw 19026	Treelet	70-80	403 (220-750)	1816 (1500-2050)	4.5
Uw 20189	Tree	100-140	386 (210-600)	1412 (920-2000)	3.7
Uw 18736	Liana	150-250	434 (250-550)	880 (500-1400)	2.0
Uw 22771	Liana	120-200	350 (250-470)	933 (650-1200)	2.7
Uw 22804	Liana	130-220	420 (240-550)	1293 (750-1650)	3.1
Uw 23258	Liana	100-300	374 (230-550)	1006 (710-1260)	2.7

wood of the vines, the fiber-tracheids are not only shorter but also have a slightly wider lumen and a slightly thinner wall with more numerous bordered pits, particularly on the tangential walls; furthermore, they are often crooked and twisted. The occurrence of shorter, thin-walled, more densely pitted fiber-tracheids in the vining specimens of *A. grandifolia* is in accordance with the general trend for imperforate elements of climbing dicotyledons, as pointed out by Carlquist (1975). Within a family such differences in trends between lianas and trees are usually encountered in different members of a genus (e.g., *Strychnos*) (Mennega, 1980). In this case it is interesting to observe two trends within the same species.

PHYLOGENETIC TENDENCIES

From an evolutionary point of view, little can be offered. The difficulties of comparing woods (particularly lianas) with abnormal secondary growth with normal wood has been pointed out before (see, for example, Garratt (1933)). Ayensu and Stern (1964), in their paper on the anatomy and ontogeny of the stem of the Passifloraceae, discuss at some length the physiological adaptation of the stem in the climbing species. They consider the broad vessels, the relatively short vessel members, and the presence of fiber-tracheids and tracheids to be related to the special problems of the water-conducting system in lianas. They indicate that the wood structure of the trees of the family must be examined for anatomic modifications related to phylogenetic specialization.

Among the Menispermaceae, as in the Passifloraceae, trees, shrubs, and lianas occur. In the menisperms, however, abnormal structure is present in the arborescent species as well as in the vines. If the species with abnormal growth (in the sense of the presence of supernumerary cambia) are compared to those without it, there are no important differences in the structure of the secondary wood or in the cellular components of the tissues.

The vessels in the arborescent species show only a few indications of a primitive state. For example, scalariform perforation plates—seldom present in lianas (Carlquist, 1975) and therefore hardly to be expected in the climbing species—are not present in the arborescent species. Other indications of a less advanced state, such as scalariform or opposite intervacular pitting, are also absent, and the vessel elements are not particularly long. The predominance of isolated vessels is a primitive character, as are the fiber-tracheids that constitute the imperforate tracheary elements. The absence of rays within the bundles cannot be compared to a complete absence of rays, usually considered to be a character of high specialization, but as Barghoorn (1941) discussed in his paper on the loss of rays and anomalous secondary growth, here it cannot be considered as an indication of specialization. Although rays are very scarce, one or two narrow ones may occasionally be present in the widest bundles of some species, giving the impression that it is the influence exerted by the neighboring cells that induces the formation of some ray tissue.

Thus the Menispermaceae, considered as one of the basal families in most classifications, has few really primitive features in its wood anatomy, unless the wide rays of the species without abnormal secondary growth are considered to be a less advanced character.

RELATIONSHIP WITH OTHER FAMILIES

According to most systems of classification, the Menispermaceae are placed near the Berberidaceae and the Lardizabalaceae in the order Ranales. At first glance, the resemblance between the Berberidaceae and the Menispermaceae is not striking except for the unusual yellowish green color that woods of a number of menisperms from various genera (TABLE 1) have in common with the Berberidaceae. However, when other features (e.g., the occurrence and more or less pronounced tangential arrangement of large and narrow vessels, and the large rays composed of irregularly sized procumbent cells, which never border on the vessels) are examined, more similarities between the two families become evident. Also, the pith of the woody members of the Berberidaceae consists of two different layers: a large-celled central core and, on the periphery, smaller cells with thicker, pitted walls. In herbaceous genera of the family (e.g., *Podophyllum*), the vascular bundles are scattered in the pith (Metcalfe & Chalk, 1950). The few scattered bundles noticed in the pith of *Borismene* may indicate relationship.

In the Lardizabalaceae the stem anatomy (particularly the form of the bundles, the structure of the pith, and the large medullary rays) of the liana *Akebia* closely resembles that of a young menisperm. However, new cambia are not formed. Another difference is found in the scarcity of the paren-

chyma, which is restricted to a few scattered and occasional paratracheal strands.

Additionally, the large, gashlike pits near the ends of the vessel members, which are so characteristic for all menisperms, are absent in both the Berberidaceae and the Lardizabalaceae. Such pits are, however, known in *Ocotea rodiaei* and *O. venenosa* (Kostermans *et al.*, 1969) of the less closely related Lauraceae.

SIMILARITY IN WOOD PATTERN WITH SPECIES FROM OTHER FAMILIES

The typical menispermaceous pattern as seen in cross section is also present in the lianas of the genus *Gnetum* (Gnetaceae). For example, on inspection with a hand lens, the wood of *G. nodiflorum* matches that of the menisperms quite well; the chief difference is that in *Gnetum* the parenchyma is lacking.

Another species showing some resemblance with menisperms in cross-sectional pattern is *Lerettia cordata* of the Icacinaceae. In this liana the vascular bundles are, however, not as regularly arranged, and the fascicular rays between the bundles show a far greater diversity in width. Furthermore, the phloem "caps" are smaller and less sharply demarcated than in the Menispermaceae.

ACKNOWLEDGMENTS

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APPENDIX. Material studied.*

- Abuta brevifolia* Krukoff & Moldenke. BRAZIL: *N. T. Silva* 844 (Uw 18069), 1 × 2 cm; *N. T. Silva* 847 (Uw 18066), 1 × 1.2 cm; *N. T. Silva* 3432 (Uw 18515), 1 × 2 cm; *Prance* 11627 (Uw 18735), 1 × 1.5 cm; *Prance* 12121 (Uw 18737), 3 cm.
- A. candollei* Triana & Planchon. SURINAM: *Pulle* 337 (Uw 10651), 1.5 cm; *van Donselaar* 2364 (Uw 11295), 6 cm; *van Donselaar* 2374 (Uw 11304), 3 cm; *van Donselaar* 2960 (Uw 11948), 3.5 × 6 cm.
- A. colombiana* Moldenke. COLOMBIA: *Cuatrecasas* 14028 (Uw 18758) (type), 30 cm.
- A. fluminum* Krukoff & Barneby. PERU: *J. Schunke* V. 1971/34 (Uw 18619), 3.5 × 5 cm.
- A. grandifolia* (Martius) Sandwith. SURINAM: *Lanjouw & Lindeman* 2098 (Uw 1612), 2.5 cm, shrub; *Lindeman* 4931 (Uw 3361), 3 cm, treelet; *Lindeman* 5076 (Uw 3441), 1.5 cm, shrub; *Lindeman & Heyde* 139 (Uw 22771), 2 cm; *Lindeman & Heyde* 193 (Uw 22804), 1.5 × 2 cm; *Heyde* 651 (Uw 23258), 6 cm. BRAZIL: *Forero* 6321 (Uw 18060), 2 cm; *Krukoff* 7812 (Uw 18668), 5 cm; *Krukoff* 7641 (Uw 18748), 1.5 cm; *Krukoff* 5786 (Uw 20189), material from tree of unknown diameter; *INPA-Manaus X-4100* (Uw 18866), 4.5 cm; *Prance* 12116 (Uw 18736), 3.5 cm; *Prance* 13948 (Uw 19026), 5 cm, tree; *Prance* 18090 (Uw 20890), 2.5 cm. BOLIVIA: *Krukoff* 10954 (Uw 18757), 4 cm, shrub. PERU: *Ll. Williams* 8013 (Uw 18750), 7.5 cm, tree; *Ll. Williams* 3500 (Uw 18753), 8 cm, tree; *Ll. Williams* 4713 (Uw 18754), 6.5 cm, tree; *Ll. Williams* 2435 (Uw 18755), 7.5 cm, tree; *J. Schunke* V. 1970/25 (Uw 18074), 1 cm.
- A. grisebachii* Triana & Planchon. BRAZIL: *Krukoff* 7822 (Uw 18667), 2.3 × 2.5 cm; *Krukoff* 8660 (Uw 18664), 3 × 5.5 cm; *Krukoff* 7960 (Uw 18666). PERU: *J. Schunke* V. 5498 (Uw 20523), 2.5 × 4 cm.

*Unless otherwise stated, material is from lianas. The diameter of the stems is indicated in cm; for asymmetric stems the largest and smallest dimensions of the cross sections are given.

†Sections only.

- A. imene* (Martius) Eichler. SURINAM: *Lindeman* 6985 (Uw 4700), 4 cm. BRAZIL: *Krukoff* 8605 (Uw 18691), 10 cm. PERU: *Mathias & D. Taylor* 3660 (Uw 18520), 2 × 3.5 cm.
- A. obovata* Diels. SURINAM: *van Donselaar* 3171 (Uw 12020), 3 × 8 cm. BRAZIL: *Prance* 12437 (Uw 18738), 1.5 × 3.5 cm.
- A. pahnii* (Martius) Krukoff & Barneby. PERU: *J. Schunke* V. 1970/28 (Uw 18613), 9 cm.
- A. panurensis* Eichler. BRAZIL: *Prance* 14973 (Uw 18924), 3.4 × 6 cm; *Prance* 11575 (Uw 18734), 0.5 cm.
- A. rufescens* Aublet. FRENCH GUIANA: *Maas, Mennega, & Koek* 2188 (Uw 21098), 4 cm. SURINAM: *van Donselaar* 3832 (Uw 12356), 1.4 cm; *Maas, Mennega, & Koek* 2364 (Uw 12163), 1 cm. BRAZIL: *Krukoff* 8030 (Uw 18665), 3 × 6 cm; *Krukoff* 10652⁺ (Uw 18663); *Krukoff* 10866 (Uw 18662), 1 × 2 cm; *Krukoff* 10927 (Uw 18661), 4 × 10 cm; *Krukoff* 11083 (Uw 18660) (type), no exact dimensions available, stem over 7 cm wide; *Prance et al.* 5367 (Uw 18058), 2 × 4.5 cm; *Prance* 11036 (Uw 18730), 4.5 cm; *N. T. Silva* 3125 (Uw 18079), 5 × 6 cm; *N. T. Silva* 3433 (Uw 18519), 1 cm. PERU: *J. Schunke* V. 5168 (Uw 18926), 1.5 × 4.5 cm; *J. Schunke* V. 1970/23 (Uw 18071), 1.5 × 4.5 cm; *J. Schunke* V. 1971/38 (Uw 18623), 1.3 × 6 cm.
- A. sandwithiana* Krukoff & Barneby. SURINAM: *van Donselaar* 2928 (Uw 11941), 3.5 cm. BRAZIL: *Prance* 12461 (Uw 18739), 1 cm; *Krukoff* 7640 (Uw 18756), 3 cm.
- A. solinoesensis* Krukoff & Barneby. BRAZIL: *N. T. Silva* 842 (Uw 18064), 2 × 4.5 cm. PERU: *J. Schunke* V. 5185 (Uw 18927), 3 cm; *J. Schunke* V. 1971/31 (Uw 18616), 1.5 × 1.8 cm.
- A. velutina* Gleason. BRAZIL: *Prance & Maas* 15185 (Uw 19133), 4 × 8 cm. PERU: *J. Schunke* V. 1969/18 (Uw 18076), 2 × 2.4 cm.
- Abuta* sp. PERU: *J. Schunke* V. 1971/33 (Uw 18618), 5 × 7 cm.
- Anomospermum bolivianum* Krukoff & Moldenke. BRAZIL: *N. T. Silva* 843 (Uw 18056), 1.5 cm; *N. T. Silva* 3431 (Uw 18518), 2.3 cm. BOLIVIA: *Krukoff* 10773 (Uw 18672) (type), 2.7 cm, climbing shrub.
- A. chloranthum* Diels subsp. *chloranthum*. BOLIVIA: *Krukoff* 10639⁺ (Uw 18671).
- A. chloranthum* Diels subsp. *occidentale* (Cuatrecasas) Krukoff & Barneby. COLOMBIA: *Cuatrecasas* 15628 (Uw 18759), 3 cm.
- A. matogrossense* Krukoff & Barneby. BRAZIL: *Maguire et al.* 56807 (Uw 16524) (type), 10 cm.
- A. reticulatum* (Martius) Eichler subsp. *dielsianum* (Moldenke) Krukoff & Barneby. BRAZIL: *Prance* 12562 (Uw 18742), 2.5 cm.
- A. reticulatum* (Martius) Eichler subsp. *reticulatum*. PERU: *J. Schunke* V. 1970/29 (Uw 18614), 7 × 10 cm.
- A. solinoesanum* (Moldenke) Krukoff & Barneby. BRAZIL: *Prance* 5366 (Uw 18057), 4 cm.
- Anomospermum* sp. BRAZIL: *Krukoff* 7565 (Uw 18761), 5 × 7 cm.
- Borismene japurensis* (Martius) Barneby. PERU: *J. Schunke* V. 5388 (Uw 20524), 4 cm; *Plowman & J. Schunke* V. 7547 (Uw 25678), 3.5 cm.
- Caryomene olivascens* Barneby & Krukoff. BRAZIL: *N. T. Silva* 3117 (Uw 18070), 2 × 2.5 cm.
- Caryomene* sp. PERU: *J. Schunke* V. 1970/21 (Uw 18078), 1.5 × 2.5 cm; *J. Schunke* V. 1970/26 (Uw 18059), 2 cm.
- Chondrodendron microphyllum* (Eichler) Moldenke. *Belem* 3505 (Uw 18061), 0.6 × 1.5 cm; *Belem* 3721 (Uw 18063), 1.5 × 2.5 cm.
- C. tomentosum* Ruiz & Pavon. PERU: *J. Schunke* V. 1970/19 (Uw 18073), 3.5 cm. ECUADOR: *Gill* 20³ (Uw 18694); *Gill* 1 (Uw 18806), 2 × 3.5 cm.
- Cissampelos fasciculata* Benth. ECUADOR: *Gill* 20a⁺ (Uw 18695).
- C. pareira* L. Locality unknown: *Anonymous s.n.* (Uw 5437), 2.5 cm.
- Cissampelos* sp. BRAZIL: *Barquero* 1970/201 (Uw 18072), 1 cm.

- Cocculus laurifolius* DC. Locality unknown: *Anonymous s.n.* (Uw 5436), 4 cm.
- Coscinium fenestratum* Colebrooke. INDIA: *Anonymous s.n.* (Uw 18746), 3 cm. SRI LANKA: *Anonymous s.n.* (MADw 273610, Uw 18752), 5 cm.
- Curarea candicans* (L. C. Richard) Barneby & Krukoff. SURINAM: *Pulle 408* (Uw 13861), 1×5 cm; *LBB11304* (Uw 14670), 1×2.5 cm.
- C. tecunarium* Barneby & Krukoff. BRAZIL: *Krukoff 74* (Uw 18678), 1×3.5 cm; *Krukoff 7535*⁺ (Uw 18679); *Krukoff 7576*⁺ (Uw 18680); *Krukoff 7579*⁺ (Uw 18681); *Krukoff 7823* (Uw 18682), 1.5×2.5 cm; *Krukoff 7824* (Uw 18683), 2×6 cm; *Krukoff 7825* (Uw 18684), 2×6 cm; *Krukoff 7826* (Uw 18685), 2×7 cm; *Krukoff 7828* (Uw 18686), $1.5 \times$ over 7 cm; *Krukoff 8522* (Uw 18687), 2×10 cm; *Krukoff 8549*⁺ (Uw 18688); *Krukoff 8713*⁺ (Uw 18689); *Krukoff 8370*⁺ (Uw 18690). PERU: *J. Schunke V. 1970/24* (Uw 18054), 1×2.8 cm. ECUADOR: *Gill 6* (Uw 18692), 0.5×6 cm; *Gill 12* (Uw 18693), 0.6×6 cm; *Gill 35* (Uw 18747), 3×6 cm.
- C. toxicofera* (Weddell) Krukoff & Barneby. BRAZIL: *Prance 11272* (Uw 18732), 1 cm. VENEZUELA: *Plowman 7712* (Uw 25681), 3 cm.
- Elephantomene eburnea* Barneby & Krukoff. FRENCH GUIANA: *Oldeman B-3925* (Uw 21079) (type), 1 cm; *De Granville s.n.* (Uw 22251), piece of a trunk of unknown dimensions.
- Hyperbaena* sp. PERU: *J. Schunke V. 1971/35* (Uw 18620), 3×3.5 cm; *J. Schunke V. 1971/37* (Uw 18622), 1.5 cm.
- Odontocarya* aff. *wulfschlaegelii* (Eichler) Barneby. BRAZIL: *Prance 12545* (Uw 18741), 1 cm.
- Orthomene prancei* Barneby & Krukoff. BRAZIL: *Prance et al. 5011* (Uw 18062) (type), 0.4 cm.
- O. schomburgkii* (Miers) Barneby & Krukoff. VENEZUELA: *Breteler 3756* (Uw 11758), 3×4 cm. PERU: *J. Schunke V. 1970/20* (Uw 18075), 1.3×1.7 cm. BOLIVIA: *Krukoff 10923* (Uw 18670), 4 cm.
- Sciadotenia eichleriana* Moldenke. BRAZIL: *Krukoff 8279* (Uw 18658) (type), 5.5 cm.
- S. paraensis* (Eichler) Diels. BRAZIL: *N. T. Silva 841* (Uw 18068), 0.8×1 cm; *N. T. Silva 846* (Uw 18067), 0.6 cm; *N. T. Silva 851* (Uw 18065), 1 cm.
- S. solimoesana* Moldenke. BRAZIL: *Krukoff 8243* (Uw 18751), 3 cm; *Krukoff 8385* (Uw 18656) (type), 1×2.5 cm.
- S. sprucei* Diels. BRAZIL: *Krukoff 8020* (Uw 18657) (section only); *Prance s.n.*, collected in 1971, under *a* (Uw 18744), 0.5 cm, and *b* (Uw 18745), 0.5 cm.
- S. toxifera* Krukoff & A. C. Smith. ECUADOR: *Gill 11* (Uw 18655), 1.5×3 cm. PERU: *J. Schunke V. 5024* (Uw 18925), 2×2.5 cm; *J. Schunke V. 1971/30* (Uw 18615), 2.5×4 cm; *J. Schunke V. 1971/32* (Uw 18617), 1.6×2.5 cm; *Plowman & J. Schunke V. 7537* (Uw 25680), 1×2.2 cm.
- Telitoxicum glaziovii* Moldenke. BRAZIL: *N. T. Silva 3120* (Uw 18052), 3.5 cm; *N. T. Silva 3122* (Uw 18053), 5 cm; *N. T. Silva 3423* (Uw 18516), 5.5×5.5 cm; *N. T. Silva 3434* (Uw 18517), 5.5×6.5 cm.
- T. krukoffii* Moldenke. BRAZIL: *Krukoff 6912* (Uw 8041) (type), over 8 cm. PERU: *J. Schunke V. 1970/27* (Uw 18055), 2.5 cm.
- T. minutiflorum* (Diels) Moldenke. BRAZIL: *Krukoff 7536* (Uw 18673), diameter unknown; *Krukoff 7564*⁺ (Uw 18676); *Krukoff 7566* (Uw 18677), $2.4 \times$ over 5 cm; *Krukoff 7956* (Uw 18749), 2×4.5 cm; *Krukoff 8033* (Uw 18675), 2×6 cm; *Krukoff 8840*⁺ (Uw 18674).
- Telitoxicum* sp. PERU: *J. Schunke V. 1971/36* (Uw 18621), 2.5×5 cm.

